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FLORAL VARIATION AND TAXONOMY OF *LIMNOBIUM* L. C. RICHARD (HYDROCHARITACEAE)

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ABSTRACT

Floral and geographic evidence for infraspecific classification of the monotypic genus *Limnobium* (incl. *Hydromystria*) native to the Americas are presented. A continuum in floral form and a conspicuous overlap in patterns of flower variation between populations disclose the presence of just one latitudinally diverging species, *Limnobium spongia* (Bosc) Steudel, in which two subspecies, *L. spongia* subsp. *spongia* and *L. spongia* subsp. *laevigatum* (Humb. & Bonpl. ex Willd.) Lowden, *comb. nov.*, are recognized. Numerical analysis of floral variation in living populations and their evolutionary trends are treated for these two subspecies. Special field collections of this freshwater, non-submerged, monoecious plant were made throughout the known range of the genus in eastern United States, West Indies and South America. Population samples allowed critical morphological observations on male and female flowers, for which consistent and continuous variation was found in the form and number of petals, stamens, staminoides, stigmas, carpels and locules.

Key Words: *Limnobium,* monospecific, *Limnobium spongia* subspecies, infraspecific variation, flower variation, population diversity, aquatic plant, Americas

INTRODUCTION

The first documented field observations of floral variation in a population of this New World native aquatic plant were made by José Celestino Mutis, director of the Royal Botanical Expedition of the New Kingdom of Granada at Santa Fe de Bogotá (Bogotá), Colombia. On two occasions (April 29, 1783 and January 26, 1784) he wrote in his diary (Instituto Colombiano de Cultura

Hispanica, 1958) concerning the problems encountered to draw and classify the inconsistencies found in flowers of this interesting plant which grew then, and still abounds today, in lagoons and stagnant water about Bogotá.

Beyond his interest to conserve flowering material for drawing purposes, Mutis had collected a flower sample that enabled him to determine some of the variations that characterize the unisexual flowers of this plant for this particular locality in south America. In male flowers, Mutis found three sepals, three petals, and usually seven stamens but sometimes nine ["Por lo regular hallé siete machos y pocos de nueve. . . . casi invisibles."]. At the Madrid Botanical Garden (Spain), Mutis Plates 259, 260 & 260A (Díaz-Piedrahita, 1985, Laminas XXXV–XXXVII) show male flowers with conspicuous bilobed petals and seven stamens. Even though Mutis did not refer in his diary to these petals as being bilobed, these plates are proof that they were observed as such over two centuries ago. It is somewhat surprising to note that this obvious character has been overlooked in the herbarium and in nature until now. In the same manner, Mutis found considerable variation in female flowers ["Muchos pistilos con inconstancia"], having three sepals, apparently no petals, nine to 15 stigmatic lobes (Plate 260; shows a flower with 11 stigmatic lobes), ovary uniloculed, and fruit elongate (Plates 260 and 260A). A keen sense of observation in the field led Mutis to consider he did not have at hand ordinary flowers with a constant number of parts, but instead a highly variable plant whose classification would require further field observations.

Two decades later, flower variants of a similar plant population were observed by M. Bosc (1807) and L. C. Richard (1814; described as *Limnobium*) from a marsh in South Carolina (Basse-Caroline), United States. The male flowers were described as having three sepals, three petals, eight to 12 stamens, sometimes more [Bosc, 1807: "huit a douze étamines, et quelquefois plus, ..."] and two or three staminodes [Richard, 1814: "La colonne staminifère est terminée à son sommet par deux ou trois petits filamens tres-courts et aizus."; Planche no. 8 (B-7) shows nine stamens and at least one staminode]. Female flowers demonstrated three sepals, three petals, three staminodes [Planche (E-2) shows two of these staminodes], 12 stigmatic lobes [Bosc, 1807; ". . . six styles profundément bifurqués . . ."], ovary six loculed, fruit globose. Richard (1814) was not surprised to find male flowers with different numbers of stamens considering the number of parts found in other members of the Hydrocharitaceae.

It is only in recent years during the present decade that comparable knowledge of another population has been presented by Armando T. Hunziker (1982) from Cabalango (Dept. Punilla), Province of Córdoba, Argentina. In male flowers he counted three sepals, three petals, six stamens only and no staminodes; while, in female flowers there were three sepals, zero to three petals (sometimes one or two, rarely three), four or five staminodes (usually five in pairs or solitary opposite the sepals 2+2+1, if four, then 2+1+1 or 2+2), stigmas usually six but sometimes five (ten or 12 stigmatic lobes), ovary uniloculed with four or five inconspicuous placental partitions, and fruits oblong to ovoid. Despite his proposal to maintain the Middle and South American plant as a distinct genus (*Hydromystria*), Hunziker rightfully considered our present knowledge of this plant to be incomplete, hence a better classification depends on new data.

As such, up until now, these exact but only too few isolated field observations explain neither the extent nor the frequency of flower variants in populations that would permit the taxonomic treatment of this plant throughout its known geographic distribution in the Americas. In like manner, the same applies to herbarium studies (Díaz-Miranda et al., 1981; Cook and Urmi-König, 1983) that make assertions concerning classification of this plant based on the meager existence of dried specimens, whose exact identity based on the number of flower parts is for the most part unknown. These treatments have not recognized the occurrence of flower variants in living populations nor on dried herbarium material. Consequently, due to insufficient field studies, not only the taxonomy but the developmental biology has been misinterpreted for this plant.

At different geographical locations in the Americas, I have collected and observed the extent of variation in unisexual flowers along with their frequency of expression. The population at each locality was recognized as a dynamic and natural unit demonstrating observable biogenetic tendencies which relate to the number and kind of flower structures found in flower variants. Based on these new findings, I present a corresponding infraspecific classification.

Table 1. Traits characterizing subspecies of *Limnobium spongia.*

	Primitive	Derived
Character	*L. spongia* subsp. *spongia*	*L. spongia* subsp. *laevigatum*
Male:		
Petals	essentially unlobed	1–2 and more lobes
Stamens and staminodes	many (form 3–4 trimerous whorls)	few (form 1–3 trimerous whorls)
Female:		
Petals	3 conspicuous, essentially unlobed	apetaly common *or* petals less than 3, with 1–2 and more lobes
Staminodes	more numerous	fewer
Stigmas	many deeply-bifid (fill 2nd and 3rd trimerous stylar whorls)	fewer, somewhat less-bifid (fill 1st and 2nd trimerous stylar whorls)
Carpels	almost closed, globose ovary with 6–9 parietal placental divisions (pseudolocules, Fig. 3f–g)	open, elliptic ovary one loculed with 3–6 intruding parietal placentae (Fig. 2f–g)

SUBSPECIES CHARACTERIZED: PRIMITIVE VERSUS DERIVED TRAITS

Critical observations of floral structures disclose a consistent and continuous integration in the number and form of stamens, stigmas, staminodes, petals, locules and carpels that negates the existence in the Americas of two distinct monotypic genera, *Hydromystria* and *Limnobium* (Ascherson and Gürke, 1889; Rydberg, 1909; Díaz-Miranda et al., 1981; Hunziker, 1982), and of even the single genus *Limnobium* having two or more species (Dandy, 1959; Cook et al., 1974; Cook, 1982; Cook and Urmi-König, 1983). These new field results based on knowledge of living populations elucidate a single genus with just one very dynamic species, *Limnobium spongia* (Bosc) Steudel, for which a subspecies distinction was determined based on the inseparable nature of two diverging developmental patterns that demonstrate latitudinally phylogenetic trends for the establishment of primitive and derived floral traits. These traits which characterize the two recognized subspecies of *Limnobium spongia* are summarized in Table 1.

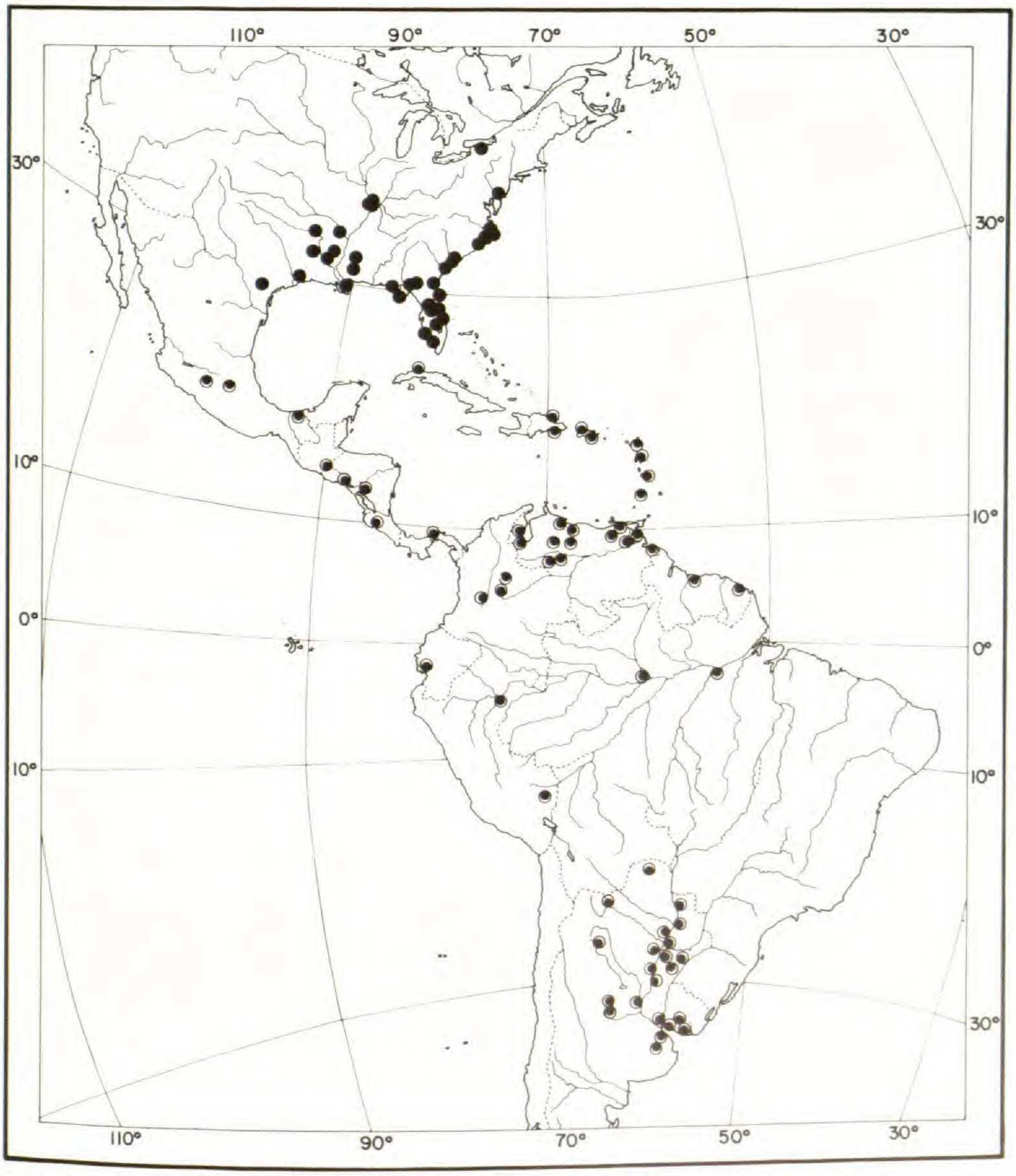

Figure 1. Distribution of the monotypic genus *Limnobium* in the Americas, showing *L. spongia* subsp. *spongia* (●) in the United States and *L. spongia* subsp. *laevigatum* (◉) in the West Indies (Greater and Lesser Antilles), Mesoamerica and South America.

Throughout its known geographic distribution in the Americas (Figure 1), *Limnobium spongia* is a species of great vegetative and reproductive plasticity. Its transitional nature is reflected by the terrestrial to aquatic habitats it occupies and by its variable imperfect floral states, which demonstrate a latitudinal continuum in specialization from one subspecies to the other.

Limnobium spongia subsp. *spongia* is more northern in latitude (limited to the eastern United States, Figure 1). In its northern-

Figure 2. Staminate and pistillate plants of *Limnobium spongia* subsp. *laevigatum* from the Dominican Republic (*Lowden 3601*): **a.** floating male plant segment with fleshy aerenchymous leaf blades and completely extended staminate pedicel; **b.** ventral view of male flower having 3 sepals, 3 petals and 6 fertile stamens; **c.** single longitudinally dehiscing mucronate-tipped stamen; **d.** female

most range (Horseshoe Lake, Illinois), this subspecies appears to have a greater number of floral parts with fewer structural modifications. Plants are generally larger, having expanded leaf blades with prominent nerves. In both male and female flowers, three unlobed petals is a relatively constant trait.

On the other hand, *Limnobium spongia* subsp. *laevigatum* occurs in more southern latitudes (south of the United States, Figure 1). Here more specialization takes place in latitudes further south (from the Dominican Republic to Argentina), where there is evidence of greater reductions in the number of floral parts. Plants are usually smaller and leaves inconspicuously nerved. More bilobed and irregularly-lobed petals are found in flowers of both sexes of this subspecies. In female flowers, apetaly and connation between concordant stigmatic lobes are considered to be highly specialized conditions, just as is reduction in fused carpel walls of fruits.

FLORAL STRUCTURES: UNISEXUAL FLOWERS

This comparative study of the gross floral morphology treats flowers collected at anthesis, which occurs between noon and late afternoon before the sun loses its thermal intensity. At this time of day in all populations, flower stalks are completely extended and a spectacular array of both male and female flowers can be observed above the water surface. Plants collected otherwise might be partly responsible for the misconception that plants are "rare" or "uncommon," stamens are "sessile" (Hauman, 1915; Hunziker, 1981), male flowers are "less common" and female inflorescences are "much more commoner" (Cook and Urmi-König, 1983).

Female and male flowers of *Limnobium* have an outer reflexed perianth whorl (Figures 2b and 2e) consisting of three, rarely four (in female flowers), purplish-tipped enrolled sepals. The petals in the alternating inner perianth whorl may be absent (Figure 2e), reduced to short rudiments (Figure 3e), *or* exceed by 1–2 mm the

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plant segment at anthesis; **e.** pistillate flower having 3 sepals, 0 petals, 3 awl-shaped staminodes (1-1-1 opposite sepals) and 12 hairy stigmatic lobes (6 deeply bifid stigmas); and **f.** lateral view of a mature elliptic pendent fruit without visible partitions in cross section, **g.** Cited specimen is deposited at UCMM.

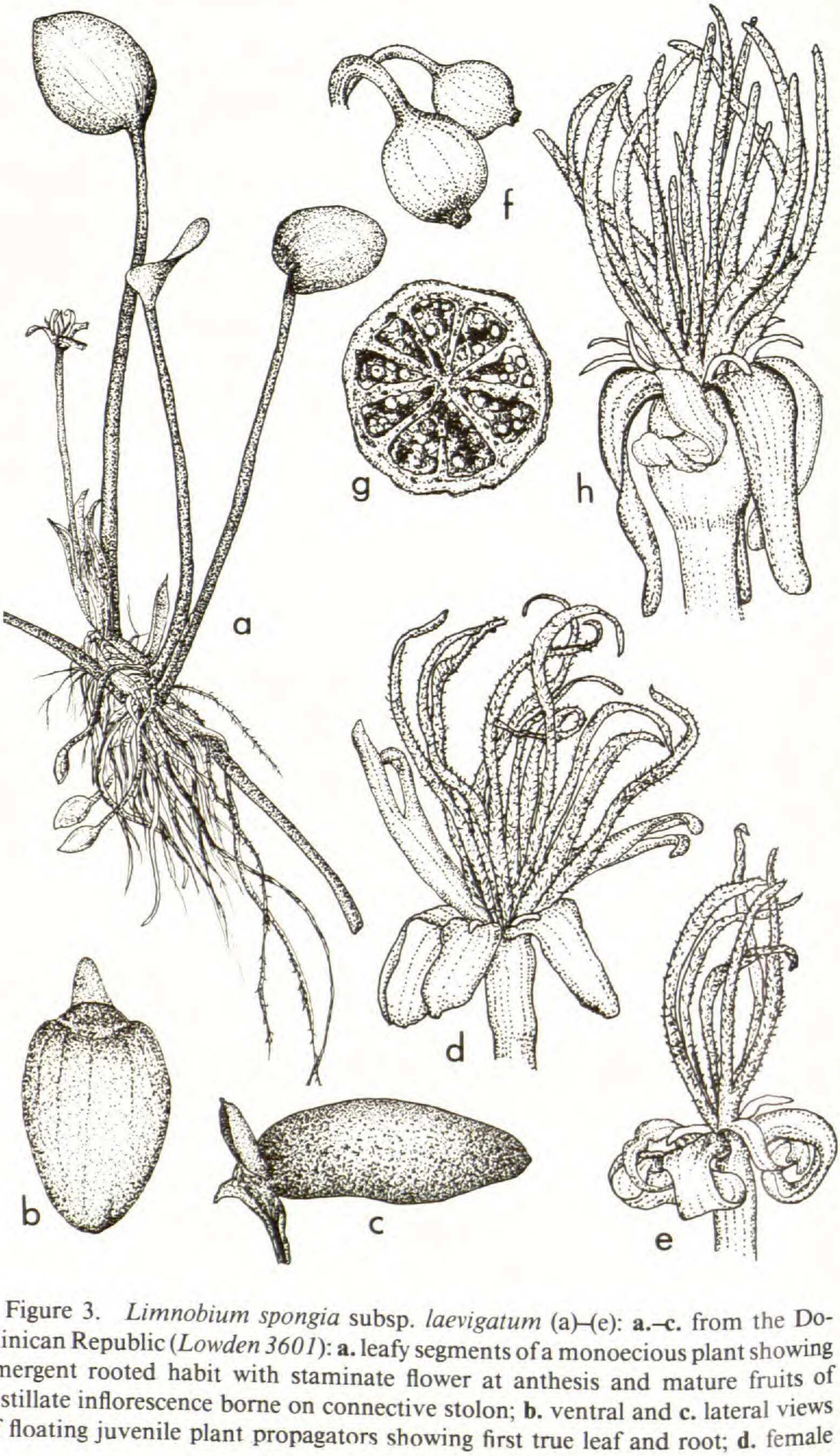

Figure 3. *Limnobium spongia* subsp. *laevigatum* (a)–(e): **a.–c.** from the Dominican Republic (*Lowden 3601*): **a.** leafy segments of a monoecious plant showing emergent rooted habit with staminate flower at anthesis and mature fruits of pistillate inflorescence borne on connective stolon; **b.** ventral and **c.** lateral views of floating juvenile plant propagators showing first true leaf and root; **d.** female

length of the sepals (Figure 4). Three erect whitish-mauve petals (Figure 4) characterize male flowers, whereas in female flowers there is an obvious reduction in the number and size of petals. In *Limnobium spongia* subsp. *spongia,* female flowers have three well-developed petals (Figure 3h), while in *L. spongia* subsp. *laevigatum* they show a conspicuous apetalous trend (Figures 2e and 3d–e).

Lobing of petals is also a significant trait in male and female flowers. The presence of unlobed petals predominates in both sexes of *Limnobium spongia* subsp. *spongia* (Figures 3h and 4a), whereas there are more bilobed petals (Figures 3d–e and 4b) and irregular petals with 3–4 minute lobes (Figure 4d) in *L. spongia* subsp. *laevigatum.* In this latter subspecies, bilobed petals appear to be more prevalent in male flowers, since fewer petals exist in female flowers due to apetaly.

Contrary to former reports (Kaul, 1968; Díaz-Miranda et al., 1981; Hunziker, 1982), my observations on male flowers reveal neither a constant number of stamens nor the absence of staminodes. A highly variable number of mucronate-tipped stamens (Figures 2c and 4) and awl-shaped staminodes (Figures 4a and 4c–d) make up the staminal column consisting of alternating trimerous whorls of connate staminal bases. These staminal parts (Figure 4) develop acropetally in the androecium where stamens or staminodes belonging to the first, third and fifth trimerous whorls are found opposite the sepals, while those in the second, fourth and sixth trimerous whorls are found opposite the petals. Stamens and staminodes become progressively smaller the higher up one moves on the staminal column, where eventually stamens may be reduced to staminodes that appear to be only anther-stalks (Figures 4a and 4c–d). In *Limnobium spongia* subsp. *spon-*

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flower from St. Lucia (*Lowden 3942*) having 3 sepals, 2 petals (deeply bifid), 4 staminodes (2 shown of 2-1-1 opposite sepals) and 11 stigmatic lobes (6 stigmas: 5 bifid and 1 unilobed); and **e.** a female flower from Argentina (*Lowden 3959*) with 3 sepals, 2 petals (1 bifid at tip), 3 staminodes (2 shown of 1-1-1 opposite sepals) and 6 stigmatic lobes (3 bifid stigmas).

Limnobium spongia subsp. *spongia* (f)–(h): **f.** two pendent globose fruits from Florida (*Lowden 3937*) showing in cross section, **g.** visible partitions of 9 pseudolocules; and **h.** female flower from Florida (*Lowden 3939*) having 3 sepals, 3 petals (2 shown), 7 staminodes (6 shown of 3-2-2 opposite sepals) and 17 stigmatic lobes (8 stigmas: 7 bifid and 1 trifid). Cited specimens are deposited at UCMM.

Figure 4. Floral parts in male flowers of *Limnobium spongia* subsp. *spongia* (a) and *L. spongia* subsp. *laevigatum* (b)–(f): **a.** 3 sepals, 3 unlobed petals and 13 fertile stamens with 3 staminodes from Illinois, U.S.A. (*Lowden 3948*); **b.** 3 sepals, 3 bilobed petals and 9 fertile stamens from the Dominican Republic (*Lowden 3947*); **c.** 3 sepals, 3 unlobed petals and 7 fertile stamens (7th just a half anther) with 1 staminode from Argentina (*Lowden 3952*); **d.** 3 sepals, 3 petals (varying

gia, the androecial column consists of 3–4 trimerous whorls of fertile stamens (Figure 4a), while in *L. spongia* subsp. *laevigatum* there are fewer fertile stamens (Figures 4b–f); just the first three trimerous whorls become filled. In northern latitudes the general tendency is toward twelve staminal parts in *Limnobium spongia* subsp. *spongia,* while in southern latitudes the trend is toward six staminal parts in *L. spongia* subsp. *laevigatum.* No real evidence was observed in fresh male flowers of pistillate parts along the central floral axis.

In female flowers no true stamens are found, only rudiments existing in one whorl as subulate antesepalous staminodes (Figure 2e). In both subspecies, these staminodes are frequently found in pairs. On the other hand, staminodes increase in numbers with a corresponding increase in the number of stigmatic lobes in *Limnobium spongia* subsp. *spongia* (Figure 3h), whereas female flowers with fewer stigmas have solitary staminodes opposite sepals in *L. spongia* subsp. *laevigatum* (Figures 2e and 3e). Even a true pistillate flower, without staminodes (Mosquera, Colombia; *Lowden 3929*), was observed in this latter subspecies.

The superior portion of the gynoecium in these imperfect female flowers consists of complete or incomplete alternating trimerous whorls having usually bifid stigmas (Figure 3e). Stigmas having one or three lobes occur infrequently. The three bifid stigmas (six stigmatic lobes) in the first (Figure 3e) and third whorls are found opposite the petals (if absent, then alternate with the sepals), while stigmas in the second trimerous whorl are found opposite the sepals and staminodes. In general, female flowers of *Limnobium spongia* subsp. *spongia* have more deeply bifid stigmas filling the second to the third trimerous stylar whorls, while fewer but somewhat less bifid stigmas fill just the first to the second trimerous stylar whorls in *L. spongia* subsp. *laevigatum.*

The inferior compound ovary bears few to many ovules borne on intruding parietal placental partitions formed by the connation of adjoining ventral carpel margins which show no signs of complete closure. The number of stigmas and placental projections is

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from 2–4 lobed) and 6 fertile stamens with 1 staminode from Colombia (*Lowden 3933*); **e.** 3 sepals, 3 unlobed petals and 6 fertile stamens from the Dominican Republic (*Lowden 3601*); and **f.** 3 sepals, 3 petals (2 slightly bilobed) and 5 fertile stamens from Argentina (*Lowden 3950*). Cited specimens are deposited at UCMM.

indicative of the number of fused carpels. The almost-closed carpels of the globose fruits (Figures 3f–g) in *Limnobium spongia* subsp. *spongia* have six to nine parietal placental divisions (pseudolocules), while the open carpels of elliptic fruits (Figures 2f–g) in *L. spongia* subsp. *laevigatum* have just one locule with usually three to six intruding parietal placentae.

An overall comparison of sexes in this monoecious plant (*Limnobium spongia*) reveals that male flowers more closely represent the imperfect state (unisexual), as evidenced by absence of pistillate parts, whereas female flowers present with great consistency an ancestral whorl of staminal rudiments opposite sepals, thus calling attention to a previous bisexual origin. Staminodes are well-developed in both sexes, yet frequently overlooked.

DIVERSITY IN POLLINATION MECHANISMS

Contrary to former belief (Cook, 1982; Cook and Urmi-König, 1983), the pollination mechanism in the genus *Limnobium* is not constant as in other genera of the Hydrocharitaceae. In this family, where the primitive nature of *Limnobium* is well known, it is not surprising to find a variety of pollination mechanisms (Hauman, 1915), depending on which floral modifications are present. As such, the sexual structures evolving in these imperfect flowers present a specialization in pollination mechanisms.

My field experience indicates that wind and insects appear to be the principal agents of pollination in both subspecies of *Limnobium spongia.* The slightest movement of the extended male pedicels (Figure 2a) brings down showers of sulfur-colored pollen onto the plumose stigmatic lobes of the shorter-stalked female flowers (Figure 2d). Powdery pollen masses reaching the water surface even float to stigmas of partially submerged female flowers. In nature, large numbers of minute aphid nymphs (*Aphididae*) and their predators, the Ladybird beetles (*Coccinellidae*), are frequent visitors that settle on the floral parts at anthesis.

Pollination by wind (anemophily) is most likely more effective in *Limnobium spongia* subsp. *spongia* where fertile stamens and stigmas are more abundant. On the other hand, in the more specialized flowers of *L. spongia* subsp. *laevigatum* insect (entomophily) and even surface pollinations might be more effective due to the reduction in the amount of pollen and stigmatic surfaces in these flowers having fewer sexual parts.

FLORAL VARIATION AND CHROMOSOME COUNTS

Cook and Urmi-König (1983) pointed out that in the Hydrocharitaceae, "one may find a greater degree of variation sometimes in a single species," such as in *Ottelia alismoides* (L.) Persoon which has "3–12 stamens, 3–10 carpels and may or may not develop dissepiments." They considered that this range of variation exceeded that found in *Limnobium.*

My field study reveals that *Limnobium* is just as, or even more, variable than *Ottelia alismoides. Limnobium spongia* has 3–14 stamens and 3–10 carpels with or without developed dissepiments. Considerable aneuploidy occurs in both of these species. As such, variation is even more accentuated in *Limnobium* where chromosome counts can be correlated with morphology and geography, while in *Ottelia alismoides* attempts to find correlations of this nature have failed (Cook and Urmi-König, 1984).

In *Limnobium* there exists a definitive relationship between character specialization, geographic latitude and chromosome number (Table 2). Significant differences in frequencies of floral variants for given population localities permit this overall formulation of male and female flower types in relation to known chromosome reports.

Chromosome counts (Table 2) elucidate an aneuploid series ($2n = 26, 27, 28, 29$ and 30) in *Limnobium spongia.* In the northern range of the species, the base number of $x = 6$ has been reported from Paynes Prairie, Florida (Bernardello and Moscone, 1986). Here, the more primitive *L. spongia* subsp. *spongia* shows a relative constant diploid count of $2n = 24$, which corresponds with more stamens and staminodes in male flowers, while female flowers have more petals, stigmas and staminodes. On the other hand, chromosome counts from southern latitudes (Guadeloupe and Argentina) reveal plants with diploid complements of $2n = 26$–30. Frequencies for these counts (in parentheses) indicate a progressive increase in the diploid number as one goes further south where flower specialization is evidenced with fewer floral parts in plants of both sexes of *L. spongia* subsp. *laevigatum.* Supposing this to be the case, one would expect to find more counts of $2n = 30$ in plants at the southernmost extreme of the distribution of this subspecies (Figure 1; San Miguel Del Monte, Argentina).

Further studies in the genus *Limnobium* should take into account the existence of these floral types in nature. In this manner, exact relationships might be established between cytotypes and

Table 2. Relationship between character specialization, geographic latitude and chromosome number in *Limnobium spongia*.

Subspecies	Overall Floral Type	Locality & Diploid Counts
Subsp. *spongia*	male: 12 stamens, petals 1-lobed female: 3 unlobed petals, 8–9 stigmas, staminodes 2–2–2 to 3–3–2	U.S.A.: Florida Paynes Prairie; $2n = 24$ (96 cells from 68 seedlings) (Bernardello & Moscone, 1986)
Subsp. *laevigatum*	male: 6 stamens, petals 1- 2-lobed female: 0–2 petals, 1–2-lobed; 5–6 stigmas; staminodes 1–1–1 to 2–1–1	Guadeloupe: West Island, Maire-Galante; $2n = 26(2), 27(6), 28(4), 29(2), 30(1)$ (Cook & Urmi-König, 1983)
	male: 6 stamens, petals 1–2-lobed female: 0–1 petals, unlobed; 5–6 stigmas; staminodes 2–1–1 to 2–2–1	Argentina: Córdoba—Cabalango & Embalse Río III; $2n = 28$ (75 metaphase plates from 51 plants) (Moscone & Bernardello, 1985)
	male: 6 stamens, unlobed petals, rarely 2-lobed female: 0–2 petals, 1-lobed, rarely 2-lobed; 5–6 stigmas; staminodes 1–1–1 to 2–1–1	Argentina: Buenos Aires, Riachuelo; $2n = 26(4), 27(3), 28(5), 29(5)$ (Cook & Urmi-König, 1983)

their corresponding morphological floral countertypes. Field experimentation between both subspecies of *Limnobium spongia* will most likely disclose the genetic pathways existing between floral traits and chromosomal germplasm. A better understanding of these cytological and morphological variation patterns in this primitive genus would undoubtedly extend our knowledge of phylogenetic trends in the Hydrocharitaceae.

TAXONOMY AND GEOGRAPHY

Limnobium L. C. Richard, Mém. Classe Sci. Math. & Phys. Inst. France (Paris), pp. 66–67, fig. 8. 1811 (pt. 2, publ. 1814).

Hydromystria G. F. W. Meyer, Prim. Fl. Esseq. 152–153. 1818.
Jalambicea Cervantes in De La Llave & Lexarza, Nov. Veget. Descr. 2: 12. 1825.
Rhizakenia Rafinesque, Autikon Botanikon, p. 188. 1840.
Trianea Karsten, Linnaea 28: 424. 1857.
Hydrocharella Spruce ex Bentham in Bentham & Hooker, Genera Plantarum 3(2): 452. 1883.

Plants monoecious (Fig. 3a), perennial aquatic herbs, stems trailing and rooted at nodes, leaves floating (aerenchymous) or aerial, blades rounded, cordate to spatulate, principal nerves converging (Figs. 2a & 2d). Flowers imperfect (Figs. 2b & 2e), inconspicuous, true petals white-mauve, in both sexes slightly longer and rarely as broad as the green-purplish sepals (Fig. 2b), apices narrowly rounded to irregularly lobed (Figs. 3d–e & 4), *or* petals reduced to rudiments or absent only in female flowers (Fig. 2e). STAMINATE FLOWERS (Fig. 4) with stamens and staminodes glabrous, united in one staminal column arising acropetally in alternating antesepalous or antepetalous trimerous whorls (Fig. 4b), anthers much longer than broad, mucronate-tipped (Fig. 2c). PISTILLATE FLOWERS (Figs. 2e, 3d–e & 3h) with staminodes glabrous, arranged in only one antesepalous whorl (Fig. 3h), stigmas bifid nearly to the base, exceeding the length of the perianth.

In the New World, the genus *Limnobium* might be confused in North America with the European frogbit, *Hydrocharis morsus-ranae* L., which has been introduced in Ontario and Quebec, Canada (Louis-Marie, 1958; Catling and Dore, 1982). Only recently, the European frogbit has spread from these Canadian provinces to New York (Roberts et al., 1981) where the American *Limnobium spongia* (Bosc) Steudel reaches its northern limits in the eastern United States (Figure 1). Despite their vegetative similarity, these two species are morphologically distinct, based on flower characters.

The European frogbit is a dioecious plant whose showy white-yellowish flowers have broadly-rounded petals that are much longer and broader than the sepals. In male flowers, the anthers of stamens are more or less oval, nearly as long as wide, bases of filaments are united in pairs, staminodes are hairy (at times so is the filament of the innermost stamen). In female flowers the antepetalous staminodes are glandular, while the antesepalous ones are elongate and hairy; stigmas are bifid for one-half their length and much shorter than the petals.

Limnobium is a monotypic genus, widely distributed in the temperate and tropical parts of the Americas.

TYPE SPECIES: *Limnobium spongia* (Bosc) Steudel

1. **Limnobium spongia** (Bosc) Steudel, Nom. Bot. ed. 2, 45. 1841. Type basionym: *Hydrocharis spongia* Bosc, Ann. Mus. Hist. Nat. Paris 9: 396–398, pl. 30. 1807. U.S.A., "Basse Caroline," *Bosc* (G, P).

Aquatic plants, floating to emergent, forming dense floating mats or inhabiting mudflats, roots fibrous, stems stoloniferous, nodes form leafy rosettes; leaves stipulate, rounded cordate or spatulate, green-purplish, entire, with 3–7 longitudinal nerves, cross-nerves less conspicuous, floating blades usually aerenchymous with short petioles, aerial blades with longer petioles and lacking a central spongy layer. Inflorescences cyme-like, sessile or short-pedunculate, subtended as flowers by floral (spathe) bracts, lanceolate to oblanceolate, few- to many-flowered, opening usually one at a time. Flowers unisexual, pedicels extended at anthesis, reaching approx. 11.0 cm in both sexes, sepals 3–4 (usually 3), boat-shaped, wider than petals, petals 0–4 (usually 3, except for the obvious apetalous trend in female flowers south of the United States), linear to lanceolate, slightly longer than sepals, unlobed or irregularly 2–4 lobed (2-lobed petals are not uncommon). STAMINATE FLOWERS with 3–14 fertile stamens (6 or 12 common), anthers approx. 4.0 mm long with mucronate tips, longitudinally dehiscing (Fig. 2c), 0–6 awl-shaped staminodes (if present, usually one), approx. 0.5–4.0 mm long. PISTILLATE FLOWERS with 0–4 antisepalous staminodes (usually 1–2), awl-shaped, reaching 4.0 mm long, 3–10 bifid hairy stigmas (6–19 stigmatic lobes), however, 5–6 are common (10–12 stigmatic lobes). Fruits pendent, beaked at apex, elliptic to globose (Figs. 2f & 3f), many seeded, berry-like, unilocular, placentation parietal, 3–9 intruding placental partitions, mature seeds beaked and covered with trichomes, approx. 0.1–0.3 mm long, seedling propagators (Figs. 3b–c) floating and inconspicuous.

In the Americas, *Limnobium spongia* occupies a variety of ecological habitats ranging from ponds, lagoons, swamps and lakes along hilly coastal plains at sealevel to mountain plateaus reaching 3000 m (Bogotá, Colombia). However, there is apparently no variation in plants because of the change in altitude. Other aquatic plants commonly associated with *Limnobium spongia* are *Eichhornia crassipes* (Mart.) Solms, *E. azurea* (Sw.) Kunth, *Pistia stratiotes* L., *Lemna* spp., *Wolffiella* sp., *Nelumbo lutea* (Willd.) Pers., *Nymphaea* spp., *Azolla* sp., *Salvinia* sp. and *Ricciocarpus* sp.

KEY TO THE SUBSPECIES OF *LIMNOBIUM SPONGIA*

1a. Leaves cordate-based (especially in juvenile and floating blades) to rounded; fruits globose, 6–9 placental divisions; female flowers usually with 3 petals, number of bifid stigmas usually 6–9 (i.e., 12–18 stigmatic lobes); male flowers frequently have 12 fertile stamens (9–11 stamens not uncommon) .... *L. spongia* subsp. *spongia*

1b. Leaves spatulate (rarely cordate based in floating blades); fruits elliptic, 3–6 intruding parietal placentae; female flowers without petals *or* if present usually less than 3, number of bifid stigmas commonly 4–6 (i.e., 8–12 stigmatic lobes); male flowers frequently have 6 fertile stamens (7–9 stamens not uncommon) .... *L. spongia* subsp. *laevigatum*

In general, plants are larger in *Limnobium spongia* subsp. *spongia* as compared with a decrease in size and increase in number of plants per unit area in *L. spongia* subsp. *laevigatum*. Big aerial plants of the American frogbit, *L. spongia* subsp. *spongia*, reach the height of mature water hyacinth (*Eichhornia crassipes*) in rivers and lakes of Florida in the southeastern United States. Here, from the "St. John's River runs and lakes to Lake Okeechobee bays" (Bodle, 1986), these large plants of *L. spongia* subsp. *spongia* inhibit water flow or navigation and have been the target of an aquatic plant control program. On the other hand, in Colombia the smaller (less conspicuous) forms of *L. spongia* subsp. *laevigatum* flourish in drainage ditches where they recycle nutrients from wastewaters on the Bogotá Plateau.

In both subspecies there are exceptionally small flowering plants that inhabit mudflats in juxtaposition with larger aerial-flowering plants which normally float in entangled mats. The scarcity of these smaller flowering plants at northern latitudes made it impossible to determine further local relationships between plant size and number of flower parts beyond those already established for the overall distribution of each subspecies.

1a. **Limnobium spongia** (Bosc) Steudel, subsp. **spongia**, Nom. Bot. ed. 2, 45. 1841. Type basionym: *Hydrocharis spongia* Bosc.

Hydrocharis spongia Bosc. Ann. Mus. Hist. Nat. Paris 9: 396–398, pl. 30. 1807. ["Basse-Caroline"]

Limnobium bosci L. C. Richard, Mém. Classe Sci. Math & Phys. Inst. France (Paris), pp. 32–34, fig. 8. 1814 (pt. 2, 1811).

Hydrocharis cordifolia Nuttall, Gen. North Am. Pl. 2: 241. 1818.

Plants taller (reaching approx. 5 dm), leaves with 5–7 principal nerves, secondary nerves usually visible, floating and aerial leaves cordate-based or rounded. Flowers of both sexes (Figs. 3h & 4a) usually with 3 well-developed unlobed petals (female flowers rarely with 2 or 4 petals; bilobed petals infrequent in both sexes). STAMINATE FLOWERS (Fig. 4a) with 8–14 (12 usually) fertile stamens and 0–5 staminodes (frequently one or even more present) in the upper (third through the sixth) trimerous whorls of an extended staminal column (Fig. 4a). PISTILLATE FLOWERS (Fig. 3h) with more (up to 4) staminodes in groups opposite sepals, staminodes robust, stigmatic lobes numerous (commonly 12–18). Fruits globose (Figs. 3f–g; approx. 1.0–1.6 cm wide) with 6–9 parietal placental divisions or pseudolocules; at maturity the outer ovary walls decay leaving partitions embedded in a gelatinous substance.

Throughout most of its distribution, this subspecies is a frequent inhabitant of swamps of bald cypress (*Taxodium distichum* (L.) Richard). Of particular interest was an herbarium specimen collected by Rogers (*Rogers, 8773-A*) from Rankin County, Mississippi. This dried specimen of a male flower has an unusual number of staminal parts: ten stamens and nine staminodes. The innermost structure extending from the staminal column appears to be a bilobed hairy stigma. Fresh material of male and female flowers from this particular locality might make it possible to ascertain the somewhat doubtful nature of this dried flower. Up until now, this male flower is the only one which I have seen with signs of a bisexual state.

DISTRIBUTION: (Figure 1.) This subspecies is endemic to temperate and subtropical regions in the United States where it mainly occurs along the Gulf of Mexico and the Atlantic coastal lowlands from Louisiana-Florida-Delaware in the south, reaching a northernmost limit in the state of New York (Braddock Bay, Lake Ontario) in the northeast, extending to the southwest from the Mississippi River delta into Oklahoma and Texas, and in the Mississippi valley north to southern Illinois and southeastern Missouri in the midwest.

The unsubstantiated reports (Catling and Dore, 1982) from Monmouth County, New Jersey (Mackenzie, 1922; Fassett, 1957) and Lake County, Indiana (Deam, 1940) have not been included in this study, as well as specimens not seen by this author but cited by others for the states of Oklahoma (Langdon, 1959) and Kentucky (Catling and Dore, 1982).

1b. **Limnobium spongia** (Bosc) Steudel, subsp. **laevigatum** (Humboldt & Bonpland ex Willdenow) Lowden, *comb. nov.* Type basionym: *Salvinia laevigata.*

Salvinia laevigata Humb. & Bonpl. ex Willd., Sp. Pl. 5: 537. 1810. ["St. Fe de Bogotá"] (HOLOTYPE: B; ISOTYPE: P).

Hydromystria stolonifera G. F. W. Meyer, Prim. Fl. Esseq., 152–153. 1818 ["plantationis Hamburg," Guyana, Río Essequibo] (HOLOTYPE: GOET).

Jalambicea repens Cervantes in De La Llave & Lexarza, Nov. Veget. Descr. 2: 12. 1825. ["Frequentissima in defossis Mexicanis"].

Limnobium sinclairii Bentham, Bot. H.M.S. Sulphur 175. 1844. ["Guayaquil"] (HOLOTYPE AND ISOTYPE: K).

Trianea bogotensis Karsten, Linnaea 28: 424–425. 1857. ["in planitiei Bogotanae"] (ISOTYPE: US).

Limnobium stoloniferum (G. F. W. Meyer) Grisebach, Fl. Brit. West Ind. Isl. 506. 1862. ("Hab. Trinidad!, Cr.; [Guiana!]")

Hydrocharella echinospora Spruce ex Bentham in Bentham & Hooker, Gen. Pl. 3(2): 452. 1883. Brasil, ["flum. Amazonum. ad ostium flum. Solimoes"], *Spruce 1593* (HOLOTYPE: BM; ISOTYPES: G, K).

Hydrocharis stolonifera (G. F. W. Meyer) O. Kuntze, Rev. Gen. Pl. 3(3): 297. 1893. ["Concepcion de Paraguay"].

Hydromystria sinclairi (Bentham) Huaman, Anales Mus. Argent. Ci. Nat. "Bernardino Rivadavia" (Buenos Aires) 27: 326–327. 1915.

Limnobium bogotense (Karsten) Delay, Bull. Soc. Bot. France 88: 481. 1941.

Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine, Adansonia 8: 315. 1968.

Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Morton, Contr. U.S. Nat. Herb. 38: 270. 1973.

Hydromystria laevigata (Humb. & Bonpl. ex Willd.) A. T. Hunziker, Lorentzia 4: 5–8. 1981.

Hydromystria laevigata (Humb. & Bonpl. ex Willd.) Diaz-Miranda et al., Bot. J. Linn. Soc. (London) 83(4): 318. 1981.

Plants shorter (Figs. 2a, 2d, & 3a; reaching approx. 4.5 dm), leaves (Fig. 3d) with 3–5 principal nerves, secondary nerves inconspicuous, floating and aerial leaves (Figs. 2a & 2d) spatulate, rarely cordate-based. Only male flowers (Fig. 2b) usually with 3 petals (2 or 4 petals occur), while in female flowers petals reduced in size and number to the point where apetaly is common (Fig. 2e). In both sexes bilobed petals (Figs. 3d & 4b) are generally just as pronounced as unlobed petals (with an increase to 3-lobed and 4-lobed petals in female and male flowers, respectively. STAMINATE FLOWERS (Figs. 2b & 4b–f) with 3–10 (6 usually) fertile stamens and 0–3 staminodes (frequently absent but when present, one is common) in the upper (second through the fourth) trimerous whorls of the shortened staminal column (Fig. 4e). PISTILLATE FLOWERS (Figs. 2e & 3d–e) with zero (rare) or few (up to 3) staminodes opposite sepals, staminodes weak, stigmatic lobes fewer (commonly 8–12). Fruits elliptic (Figs. 2f–g; approx. 1.0–1.5 cm long to 0.4–3.5 mm wide) with 3–6 intruding parietal placentae, unilocular.

On the Caribbean islands of Puerto Rico and Martinique, I did not find any populations. In Puerto Rico, urban developments have destroyed habitats at Loiza Aldea; sugar cane plantations now extend from Arroyo to Patillas, just as rice fields and cattle pastures predominate from Vega Alta to Vega Baja and Florida. In Martinique, the ponds amongst the coastal hills have dried up and the Caravelle Peninsula today supports only a very dry bush vegetation affected by the encroaching sugar cane fields and livestock.

Deserving special mention are those herbarium materials that helped to delineate the geographic limit of *Limnobium spongia* subsp. *laevigatum* in Middle America. The drawing of the Mexican plant (*Sesse* & *Mocina,* F) shows clearly a male flower with 6 stamens and a female flower with 12 stigmatic lobes. Male specimens from Nicaragua (*Nichols 1058,* MO), El Salvador (*Rohweder,* GH) and Costa Rica (*Crow* & *Charpentier 5933,* MO) have one, two or three bilobed petals, respectively, and 6 fertile stamens. Only the specimen from El Salvador has in addition one staminode. In the Greater Antilles, a Cuban specimen (*Leon 9032,* NY) disclosed diagnostic data for both sexes. The female flower has zero petals, 4 staminodes, 6 bifid stigmas and an ovary without dissepiments, while the male flower has 7 fertile stamens. Specimens from Puerto Rico show 6 stamens (*Britton* & *Britton 7949,* NY) and elliptic fruits (*Sintenis 5779,* MO).

DISTRIBUTION: (Figure 1.) This tropical to temperate (in southern latitudes and altitudes) subspecies is found throughout the West Indies on the Caribbean islands of Cuba, Hispaniola (Dominican Republic) and Puerto Rico in the Greater Antilles, and Antigua, Montserrat, Guadeloupe, Martinique, St. Lucia and Trinidad in the Lesser Antilles; in Mesoamerica it mainly occurs along the Pacific lowlands of Mexico, Guatemala, El Salvador, Nicaragua, Costa Rica and Panama; and in South America it occurs in Colombia, Venezuela, Guyana, Surinam, French Guiana, Ecuador, Peru, Brazil, Paraguay, Uruguay and Argentina.

Worthy of mention are references to specimens from localities not personally examined but cited by other authors for Montserrat (Howard, 1979) and Trinidad (Simmonds, 1967). The existence of *Limnobium spongia* subsp. *laevigatum* in Guyana is based on the type specimen of *Hydromystria stoloniferum* ("Essequibo.") in the Grisebach Herbarium at Goettingen. Of further interest are reports of localities in southwestern Brazil (Hoehne, 1948: Corumbá and Cáceres, State of Mato Grosso), which lead one to expect further plant collecting in Brazil (Figure 1) will reveal a more than infrequent occurrence of this plant.

CONCLUSIONS

Plant collectors should recognize flower variants in nature and determine the number of flower parts along with their frequency of expression in populations. This relevant collection data should accompany locality information on herbarium labels. These kinds of field observations will be most helpful in understanding the real extent of variation in populations as compared to dried herbarium specimens which demonstrate none, or at most one, of these flower variants.

The dissemination of *Limnobium spongia* in the Americas appears to be through natural means instead of by artificial introductions. Perhaps this natural dissemination has contributed to the expression of a continuum in characters which may be observed as two diverging developmental patterns between North and South American latitudes. The overall similarity of flower variants indicates that these developmental patterns have evolved from a common gene pool.

Inbreeding studies would be of great interest for experimentally determining the exact relationships between cytotypes and their corresponding morphological floral counterparts. Populations offer the diversity in flower variants, pollination mechanisms and cytotypes that make *Limnobium spongia* an attractive laboratory organism for a better understanding of species specialization and its phylogenetical implications in the Hydrocharitaceae.

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